Singing whales generate high levels of particle motion: implications for acoustic communication and hearing?

T. Aran Mooney[1], Maxwell B. Kaplan[1], Marc O. Lammers[2,3]

[1]Biology Department, Woods Hole Oceanographic Institution, 266 Woods Hole Rd. Woods Hole, MA, USA

[2]Hawaii Institute of Marine Biology, 46-007 Lilipuna Rd. Kaneohe, HI, USA

[3]Oceanwide Science Institute, P.O. Box 61692, Honolulu, HI USA

Keywords: acoustic communication, noise, cetacean, bioacoustics, hearing, soundscape

Abstract

Acoustic signals are fundamental to animal communication and cetaceans are often considered bioacoustic specialists. Nearly all studies of their acoustic communication focus on sound pressure measurements, overlooking the particle motion components of their communication signals. Here we characterize the levels of acoustic particle velocity (and pressure) of song produced by humpback whales. We demonstrate that whales generate acoustic fields that include significant particle velocity components that are detectable over relatively long distances sufficient to play a role in acoustic communication. We show that these signals attenuate predictably in a manner similar to pressure and that direct particle velocity measurements can provide bearings to singing whales. Whales could potentially use such information to determine the distance of signaling animals. Additionally, the vibratory nature of particle velocity may stimulate bone conduction, a hearing modality similar to other low-frequency specialized mammals, offering a parsimonious mechanism of acoustic energy transduction into the massive ossicles of whale ears. With substantial concerns regarding the effects of increasing anthropogenic ocean noise and major uncertainties surrounding mysticete hearing, these results highlight both an unexplored avenue that may be available for whale acoustic communication and the need to better understand the biological role of acoustic particle motion.

Introduction

Animals can rapidly transfer a substantial amount of information acoustically if the emitted signals are conveyed with enough clarity to allow appropriate physiological and behavioral responses[1]. In air and water, most mammals are generally thought to communicate with sound by producing and perceiving periodic pressure fluctuations, and such signals can be conveyed quite efficiently. For example, humpback whale (*Megaptera novaeangliae*) song can be transmitted over large distances (>5 km) as a result of the propagating wave of acoustic pressure emitted from a singing whale[2]. There is no consensus on humpback song function, but its primary role is thought to lie in intra- and intersexual communication during the reproductive season[3,4].

While sound pressure is known to propagate over long distances, the paired acoustic particle velocity of intense, long-wavelength sounds may also be high-amplitude and therefore detectable far from the source[5,6]. For example, coral reef sounds are proposed to be detectable by particle motion-sensitive larvae at 1-2 km[7] although recent data shows proportion ranges vary based upon time of day and suggests shorter distances[8]. Instruments such as naval sonobuoys use particle motion (measured in velocity) and pressure to localize whales many kilometers away[9]. Yet among whales and other marine mammals, there is a poor understanding of the acoustic particle motion component of their sounds and its potential as a communication pathway. Recent efforts have failed to detect particle motion from whale calls even within 10 m[10], supporting the broadly held notion that this cue is significant only at close proximity to the source[11]. However, measurements of the particle motion component of whale sounds are sparse or lacking, so much uncertainty remains surrounding this potentially important acoustic cue.

As a directional cue that may propagate predictably from the whale-source, acoustic particle motion could aid whales in localizing signaling animals. Examining and quantifying these cues is important, not only to better understand fundamental communication modalities, but also to more accurately evaluate concerns about rising levels of anthropogenic noise and their effect on mysticetes.

The objectives of this work were to (a) measure the particle velocity components of acoustic signals produced by a mysticete species, the humpback whale, and (b) evaluate their potential role in mysticete communication.

Methods

Three singing whales were recorded from a vessel off Maui, Hawaii in March 2015. We recorded sound pressure and particle motion (in velocity) simultaneously, thus enabling signal comparisons. Measurements were made using a M20-PV sensor (Geospectrum Technologies) that contained three orthogonal accelerometers, an omnidirectional hydrophone (to measure acoustic particle velocity and sound pressure, respectively) and a digital accelerometer-magnetometer chip (to measure the instrument pitch, roll and heading). This tool was deployed from the boat to 10m depth using a custom noise-reduction system consisting of a series of floats which de-coupled surface-wave action from the motion sensor. The sensor was cabled to a National Instruments data acquisition board (USB-6002) and a laptop that recorded and provided near real-time, calibrated particle velocity and pressure measurements. Each whale was recorded in a series of 5-min recording bouts at close range (ca. 20-200 m). Particle velocity data were corrected for pitch, roll, and yaw, and the azimuth and elevation of individual whales were computed relative to the sensor's orientation respective to magnetic north[12,13].

Results

High levels of acoustic particle velocity were observed in all focal recordings. The magnitude of the acoustic particle velocity signal was substantial (median -103.8 dB re 1 m/s) for song components with a median pressure of 137.4 dB re 1 µPa (ambient particle velocity levels of Maui waters were -133.9 to -134.1 dB re 1 m/s). The drift of the vessel and deployed sensor correspond with systematic changes in the particle velocity and sound pressure received levels of -120.1 to -87.9 dB re 1 m/s and 120.3 to 156.7 dB re 1 µPa (min-max), respectively. While the sound levels of humpback song components can differ, the majority of this increase and decrease likely reflects the change in position and distance of the whale relative to our sensor. This is supported by the fact that pressure was strongly correlated with the particle velocity (Fig 2a,b). Indeed, when data from all 3 whales were compiled, sound pressure and particle velocity varied in a positive and relatively predictable linear relationship fluctuating around a 1:1 line ($y = 0.7891x - 211$, $r^2 = 0.79$; Fig 2c).

For the first two animals, the boat and sensor drifted particularly close to or over the singing whale. This is reflected by the increase and subsequent decrease in sound level (pressure and particle velocity) seen in whale 1 and the 1st and 3rd recording sessions of whale 2. The third whale was more difficult to track from the surface, thus recordings were made some distance away (ca. 100-200 m), yet the particle velocity components were clearly measurable (Fig 2).

Finally, while we could not usually observe the whales visually while they were underwater, we could calculate the bearing of the song cues recorded (Fig 2d,e). A typical portion of the bearing from a song segment is shown in Figure 2. While there was some variation in elevation, it was generally limited, suggesting little change in depth (relative to the sensor) for this singing whale, at this point-in-time. The focal song-cues (higher amplitudes; warmer colors) and additional environmental noises were in approximately the same vertical elevation. In comparison, azimuth values varied to a greater extent. However, we obtained consistent bearings of the focal whale's song, shown by the highest amplitude signals occurring around 50-80°. There were additional, lower amplitude sound sources (cooler colors) at different bearings, which contributed to the variability in azimuth, suggesting that ambient noise levels might affect a whale's ability to localize sources using particle motion if masking is taking place.

Discussion

These results clearly demonstrate that the particle velocity component of humpback whale song is a high-amplitude acoustic cue available to nearby animals. Because there was uncertainty about the precise position of the singer relative to the sensor, distances between the sensor and singing whales were not characterized, preventing source level and true propagation measurements. For example, distance-related sound level variations in particle velocity were correlated with variations in pressure levels and attenuated in a predictable manner, suggesting that particle motion generated by a singer might provide comparable or additional information about the singer's distance to listening whales [14,15]. Furthermore, unlike sound pressure, particle velocity is a vector quantity that allows for bearing estimation. Thus, theoretically, particle motion could aid in loudness perception and assessments of distance and bearing. With sufficient amplitudes, it seems possible that whales could use particle motion to localize/track conspecifics[4].

Notably, to detect this velocity signal it was critical to minimize overall movement of the accelerometers (reducing surface wave action and pull from the cable/buoys) which could easily have swamped the particle velocity signal detection in related efforts[10]. While there was a positive correlation with particle velocity magnitude and pressure, the relationship was not equal in all directional axes (the shape of the individual velocity signals was not identical to the pressure signals). This may be a result of the directional component of the accelerometer sensor compared to the omni-directional hydrophone, as well as some small near-field constructive-destructive variability of both the pressure and particle velocity signals.

How sound is received within a mysticete's head and transmitted to its cochlea has been a subject of historical debate[16,17]. While current hearing models assume a pressure stimulus to model sound pathways, ossicle vibration, and middle-ear chain movement[18], sound pressure is theoretically not the most efficient means of transferring acoustic energy into physical movement of the ossicles, middle ear bones or oval window structures. An impedance mismatch almost certainly increases (impairs) hearing sensitivity estimates, particularly at lower frequencies[18]. The tympano-periotic structures of mysticetes are fused and directly coupled to the skull (i.e., not acoustically isolated as in odontocetes) which strongly suggests that bone conduction plays at least some role in their hearing pathway[19-21]. The high particle velocities energy described here might be capable of inducing both ossicle vibration and middle-ear transduction proposed elsewhere[18,22]. It also revises classic notions that "In mysticetes, bone and soft tissue conduction are likely"[19] as this claim was specifically made in reference to receiving pressure waves; here we suggest that there may be a dual function in both bone and soft tissue pathways also conducting particle motion. Such a pressure-particle motion detection capability, along with directionally sensitive receptors and/or spatially segregated networks of independent receptors (to provide timing cues), might enable determining sound-source direction[21,23]. Notably, particle velocity and bone conduction support a common mode of hearing with other low-frequency ears of large terrestrial, subterranean and other aquatic animals[24-27]. Precise auditory mechanisms vary or are unknown but often include hypertrophied auditory ossicles (as in some mammals) or impedance differences of the otoliths and the surrounding tissue-water (as in fish). For example, the hippo, elephant and elephant seal use bone conduction at least in part (generated via particle motion or a vibratory stimulus) as a mode of hearing[24,25,28]. These animals are also closely related to mysticetes[29,30]. Currently, we do not know whether or how mysticetes detect particle motion; future experiments should be considered to test this potential modality. Notably, particle motion hearing does not preclude pressure detection, as many of these mammals detect both stimuli[24-27].

These data suggest that we must consider and quantify the particle motion component of anthropogenic noise sources as a potential masker of hearing and communication, or its potential to induce stress, behavioral responses or other auditory impacts[31,32]. Human-produced noise is increasing in the ocean, particularly at low frequencies [33]. This noise can have deleterious impacts on sound-sensitive marine mammals, including mysticetes[31,34]. Noise is consequently of substantial concern to the conservation and management of endangered mysticete species for which we have few data on sound use, hearing and communication. We would expect to find similar acoustic energy patterns generated by other mysticetes, thus similar communication questions and noise concerns are likely to apply to other whale species with broad implications. Having shown here that particle motion is an available acoustic communication pathway, there is now a need to quantify this signal’s biological function, effective transmission distances, and its potential role in noise-related impacts in mysticetes.

Ethics. Research protocol was approved under the WHOI IACUC ID number:21105 and data were collected under NMFS permit #: 14682 to M.O.L.

Data accessibility. Data were made freely accessible in the DRYAD Data Repository dx.doi.org/10.5061/dryad.34s86[13].

Authors' contributions. Conceived experiments: T.A.M. and M.B.K. Experimental design and data collection: T.A.M., M.B.K. and M.O.L. Wrote/revised article for intellectual content: T.A.M., M.B.K. and M.O.L. All authors agree to be held accountable for the content and approve the final version of the manuscript.

Competing interests. We have no competing interests.

Funding. WHOI's Independent Study Award to T.A.M.

Acknowledgements. We thank W. Zimmer for his analysis advice.

Table 1. Particle velocity recording summary.

	No. recording bouts	Total recording durations (min)	Particle velocity in dB re 1 m/s		
			Max.	Min.	Median
Whale 1	2	10	-91.6	-109.8	-97.9
Whale 2	4	20	-87.9	-120.1	-104.5
Whale 3	1	5	-100.3	-113.6	-105.6
Combined	2	10	-87.9	-120.1	-103.8

Figure 1. Acoustic song data obtained for a singing humpback off Maui, HI in March 2015 (a) Spectrogram of a portion of the humpback song, (b) sound pressure waveform and x, y, z (c,d,e) particle velocity waveforms of that song section recorded on the M20 PV sensor. Sound pressure varied with song unit (a-b) and particle velocity was anisotropic across the x, y, and z-axes (c-e), with the highest amplitude velocity recorded on the y axis and the lowest on the z-axis (up-down).

Figure 2. (a) Sound pressure and (b) the particle velocity magnitudes of the three humpback whales recorded. The pressure and particle motion varied within and among deployments as whale song units changed levels and the boat drifted away from the whale. (c) Yet, the relationship was roughly linear, fluctuating around a 1:1 line ($r^2 = 0.79$) suggesting a strong predictable relationship between pressure and particle motion. (d,e) Bearing of the singing humpback from the sensor plotted in sound pressure level for the 21 s of song shown in Fig 1, plotted in Elevation (d) and Azimuth (e) with respect to the sensor's position and magnetic north. While there was some variation in depth, it was generally small. Azimuth of the whale (yellow-high amplitude) values were similarly consistent but fluctuations were noted from additional (low-amplitude) sources at other angles.

References

[1]Bradbury, JW & Vehrencamp, SL. 1998 *Principles of animal communication*. Sunderland, MA, Sinauer Associates, Inc.; 882 p.

[2]Au, WW, Pack, AA, Lammers, MO, Herman, LM, Deakos, MH & Andrews, K. 2006 Acoustic properties of humpback whale song. *J. Acoust. Soc. Am.* **120**, 1103-1110.

[3]Tyack, P. 1981 Interactions between singing Hawaiian humpback whales and conspecifics nearby. *Behav. Ecol. Sociobiol.* **8**, 105–116.

[4]Darling, JD, Jones, ME & Nicklin, CP. 2012 Humpback whale (*Megaptera novaeangliae*) singers in Hawaii are attracted to playback of similar song (L). *J. Acoust. Soc. Am.* **132**, 2955-2958.

[5]Urick, RJ. 1983 *Principles of underwater sound*. New York, Mc-Graw-Hill; 423 p.

[6]Wahlberg, M, Schack, H, Wilson, M, Bejder, L & Madsen, PT. 2008 Particle acceleration noise generated by boats. *Bioacoustics* **17 (Special Issue)**, 148-150.

[7]Radford, CA, Tindle, CT, Montgomery, JC & Jeffs, AG. 2011 Modelling a reef as an extended sound source increases the predicted range at which reef noise may be heard by fish larvae. *Mar. Ecol. Prog. Ser.* **438**, 167-174. (doi:doi: 10.3354/meps09312).

[8]Kaplan, MB & Mooney, TA. 2016 Coral reef soundscapes do not propagate that far. *Scientific Reports* **6**, 31862. (doi:10.1038/srep31862).

[9]D'Spain, GL, Hodgkiss, WS, Edmonds, GL, Nickles, JC, Fisher, F & Harriss, RA. 1992 Initial analysis of the data from the vertical DIFAR array. In *OCEANS'92. Mastering the Oceans Through Technology* (ed. IEEE), pp. 346-351.

[10]Goldbogen, JA, Stimpert, AK, DeRuiter, SL, Calambokidis, J, Friedlaender, AS, Schorr, GS, Moretti, DJ, Tyack, PL & Southall., BL. 2014 Using accelerometers to determine the calling behavior of tagged baleen whales. *J. Exp. Biol.* **217**, 2449-2455.

[11]Kalmijn, AD. 1988 Acoustic and hydrodynamic field detection. In *Sensory biology of aquatic animals* (eds. J. Atema, R.R. Fay, A.N. Popper & W.N. Tavolga), pp. 83-131. New York, Springer-Verlag.

[12]Zimmer, W. 2011 *Passive Acoustic Monitoring of Cetaceans*. Cambridge, UK, University of Cambridge Press.

[13]DRYAD_Raw_data_repository:dx.doi.org/10.5061/dryad.34s86.

[14]Naguib, M & Wiley, RH. 2001 Estimating the distance to a source of sound: mechanisms and adaptations for long-range communication. *Anim. Behav.* **62**, 825-837.

[15]Mercado III, E, Schneider, JN, Green, SR, Wang, C, Rubin, RD & Banks, PN. 2007 Acoustic cues available for ranging by humpback whales. *The Journal of the Acoustical Society of America* **121**, 2499-2502.

[16]McCormick, JG, Wever, EG, Palin, J & Ridgeway, SH. 1970 Sound conduction in the dolphin ear. *J. Acoust. Soc. Am.* **48**, 1418-1428.

[17]Yamato, M, Ketten, DR, Arruda, J, Cramer, S & Moore, K. 2012 The auditory anatomy of the minke whale (Balaenoptera acutorostrata): a potential fatty sound reception pathway in a baleen whale. *Anat. Rec.* **295**, 991-998.

[18]Cranford, TW & Krysl, P. 2015 Fin Whale Sound Reception Mechanisms: Skull Vibration Enables Low-Frequency Hearing. *PloS one.* **10**, e0116222.

[19]Ketten, DR. 1997 Structure and function in whale ears. *Bioacoustics* **8**, 103-135.

[20]Nummela, S, Thewissen, J, Bajpai, S, Hussain, T & Kumar, K. 2007 Sound transmission in archaic and modern whales: anatomical adaptations for underwater hearing. *Anat. Rec.* **290**, 716-733.

[21]Schneider, JN, Lloyd, DR, Banks, PN & Mercado, E. 2014 Modeling the utility of binaural cues for underwater sound localization. *Hear. Res.* **312**, 103-113.

[22]Tubelli, AA, Zosuls, A, Ketten, DR, Yamato, M & Mountain, DC. 2012 A prediction of the minke whale (Balaenoptera acutorostrata) middle-ear transfer function. *J. Acoust. Soc. Am.* **132**, 3263-3272.

[23]Mercado III, E. 2014 Tubercles: What Sense Is There? *Aquat. Mamm.* **40**, 95.

[24]O'Connell-Rodwell, CE. 2007 Keeping an "ear" to the ground: seismic communication in elephants. *Physiology* **22**, 287-294.

[25]Barklow, WE. 2004 Amphibious communication with sound in hippos, Hippopotamus amphibius. *Anim. Behav.* **68**, 1125-1132.

[26]Mason, MJ. 2003 Bone conduction and seismic sensitivity in golden moles (Chrysochloridae). *J. Zool.* **260**, 405-413.

[27]Kastak, D & Schusterman, R. 1999 In-air and underwater hearing sensitivity of a northern elephant seal (Mirounga angustirostris). *Can. J. Zool.* **77**, 1751-1758.

[28]Reuter, T, Nummela, S & Hemilä, S. 1998 Elephant hearing. *J. Acoust. Soc. Am.* **104**, 1122-1123.

[29]Geisler, JH & Theodor, JM. 2009 Hippopotamus and whale phylogeny. *Nature (London),* **458**, E1-E4.

[30]Hoelzel, AR. 2009 *Marine mammal biology: an evolutionary approach*, John Wiley & Sons.

[31]Southall, BL, Bowles, AE, Ellison, WT, Finneran, JJ, Gentry, RL, Greene Jr, CR, Kastak, D, Ketten, DR, Miller, JH, Nachtigall, PE, et al. 2008 Marine mammal noise exposure criteria: Initial scientific recommendations. *Aquat. Mamm.* **33**.

[32]Nedelec, SL, Campbell, J, Radford, AN, Simpson, SD & Merchant, ND. 2016 Particle motion: the missing link in underwater acoustic ecology. *Methods Ecol. Evol.*

[33]McDonald, MA, Hildebrand, JA & Wiggins, SM. 2006 Increases in deep ocean ambient noise west of San Nicolas Island, California. *J. Acoust. Soc. Am.* **120** 711-717.

[34]Di Iorio, L & Clark, CW. 2010 Exposure to seismic survey alters blue whale acoustic communication. *Biol. Lett.-(UK)* **6**, 51-54.

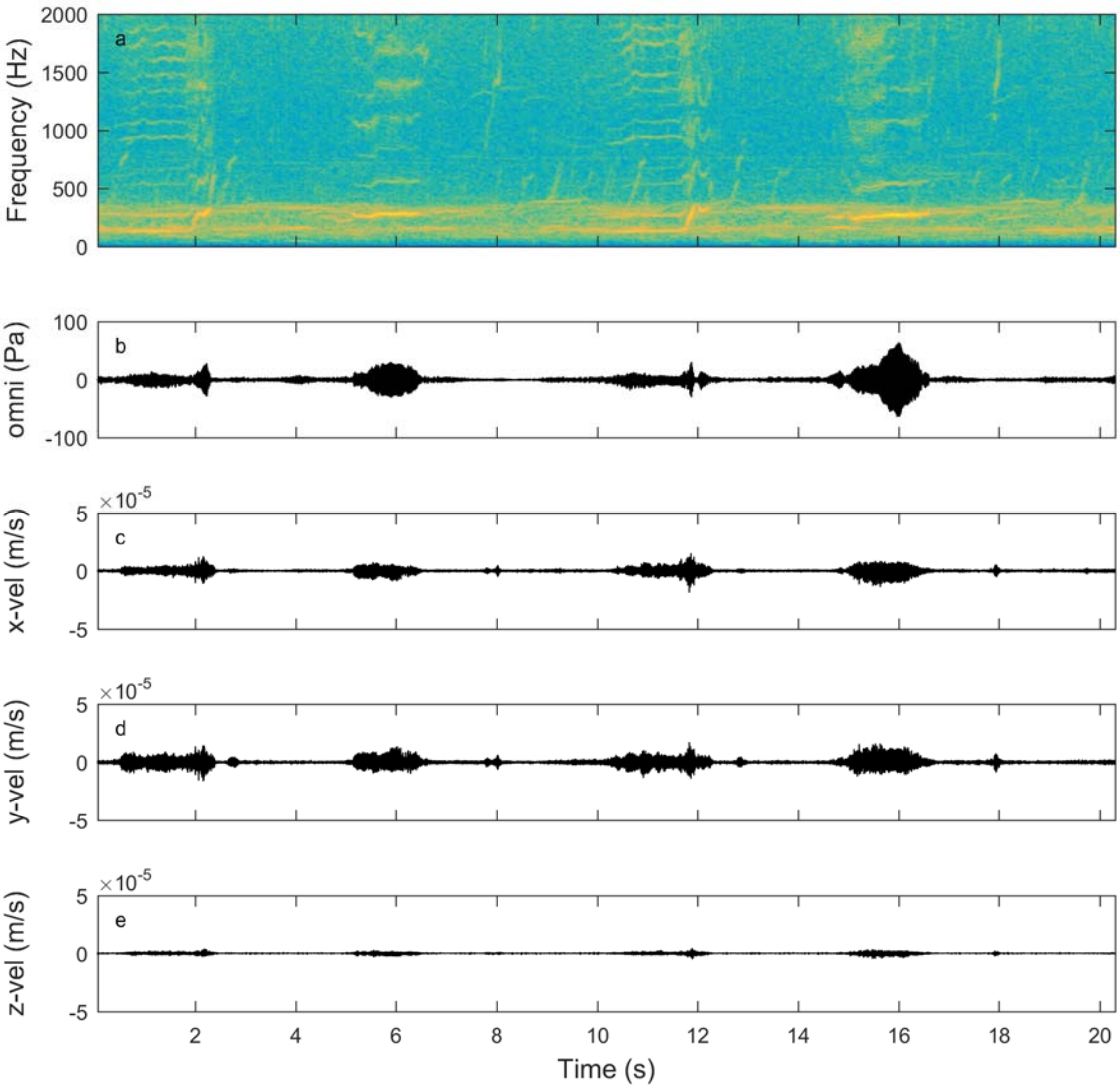

2000
1500
1000
500
0
Frequency (Hz)
a
100
0
-100
omni (Pa)
b
×10^-5
5
0
-5
x-vel (m/s)
c
×10^-5
5
0
-5
y-vel (m/s)
d
×10^-5
5
0
-5
z-vel (m/s)
e
2
4
6
8
10
12
14
16
18
20
Time (s)

Figure 1.

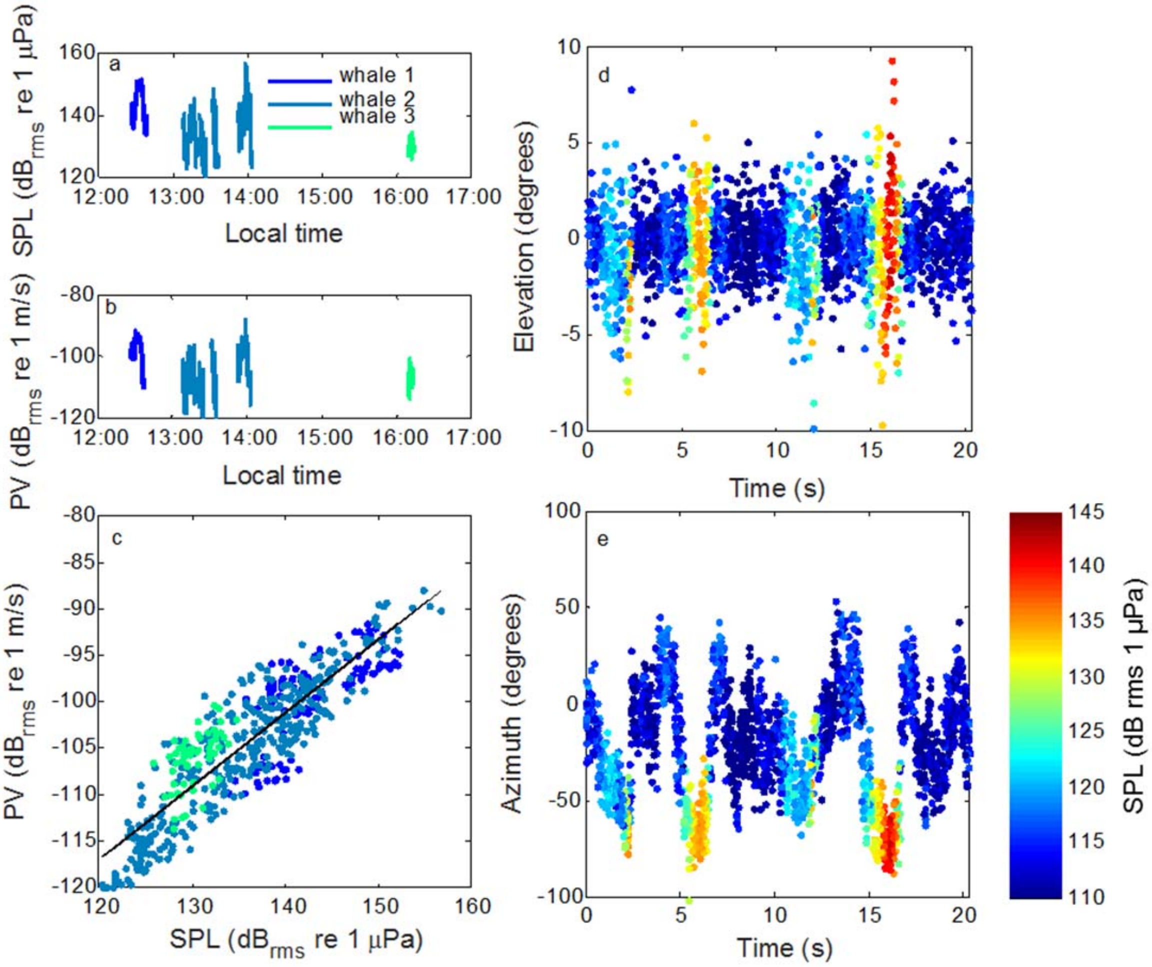

a
whale 1
whale 2
whale 3
SPL (dB$_{rms}$ re 1 μPa)
160
140
120
12:00
13:00
14:00
15:00
16:00
17:00
Local time
b
PV (dB$_{rms}$ re 1 m/s)
-80
-100
-120
12:00
13:00
14:00
15:00
16:00
17:00
Local time
c
PV (dB$_{rms}$ re 1 m/s)
-80
-85
-90
-95
-100
-105
-110
-115
-120
120
130
140
150
160
SPL (dB$_{rms}$ re 1 μPa)
d
Elevation (degrees)
10
5
0
-5
-10
0
5
10
15
20
Time (s)
e
Azimuth (degrees)
100
50
0
-50
-100
0
5
10
15
20
Time (s)
SPL (dB rms 1 μPa)
145
140
135
130
125
120
115
110

Figure 2.

Supplemental Material

Singing whales generate high levels of particle motion: implications for acoustic communication

T. Aran Mooney, Maxwell B. Kaplan and Marc O. Lammers

Biology Letters

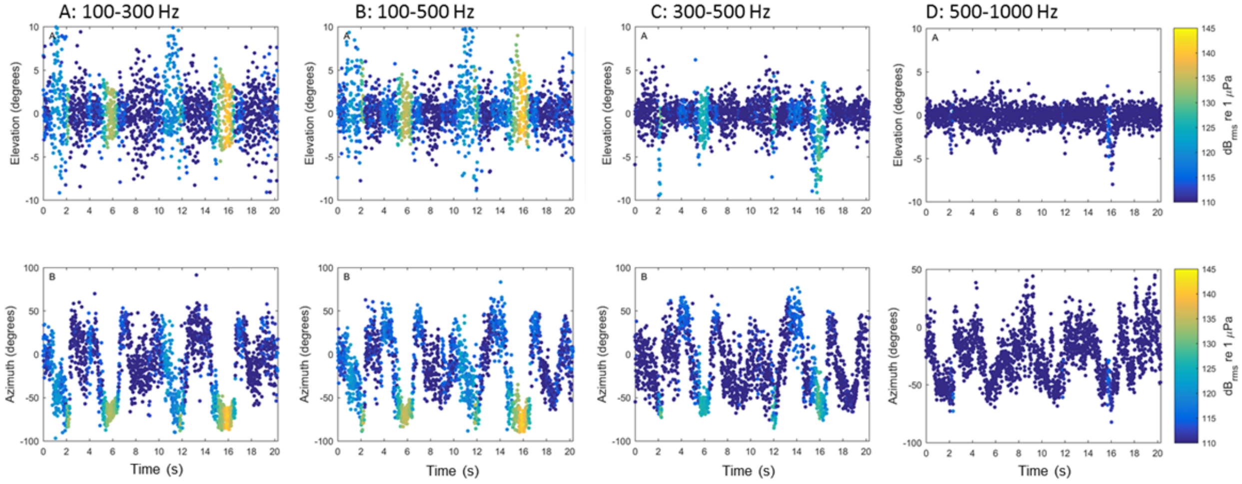
M20 Specifications

The M20 Particle Motion Sensor (Geospectrum Technologies, Canada) is designed to measure 3-D particle motion and acoustic pressure in a broad range of environments. The M20 utilizes three vector sensors and an omnidirectional sensor to provide information on direction in the horizontal plane. Specifically, it contains accelerometers housed within pressure vessels, which are oriented in the X, Y, and Z directions. The omnidirectional hydrophone is used to resolve the directional ambiguity. To correlate the data back to magnetic north and the vertical, the M20 contains a three axis roll- pitch-yaw (RPY) sensor. It has been used in prior studies to measure particle motion and pressure studies [1-4]. Its specifications as defined by the manufacturer include a useful frequency range from 1-3000 Hz, operating depth up to 300 m, operating temperature from -40 to 70° C, 127 mm dia, and 165 mm length. The accelerometers have a particle velocity peak sensitivity of -41 dB V re 1 m/s at 960 Hz, decreasing ca. linearly to -67 dB at 100 Hz, and -54 dB at 3000 Hz. The omnidirectional hydrophone has a similarly shaped response curve with a peak of -165 dB V re 1 µPa sensitivity at 960 Hz decreasing ca. linearly to -191 dB at 100 Hz, and -177 dB at 3000 Hz. Further information can be found at http://geospectrum.ca/hydrophones/m20-bottom-mount-system/.

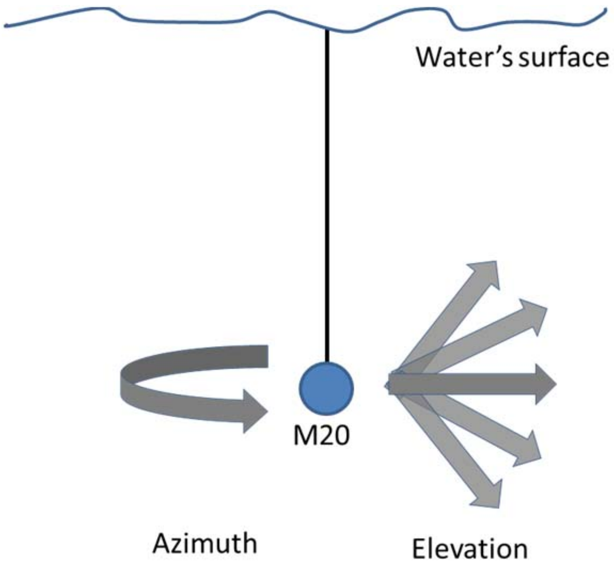
The M20 was calibrated using a shaker table and using an in-water calibration in the near field using an acoustic pressure transducer as a reference. These two sources of data are then combined into a calibration curve by comparing to a standard measured in the free field.

Azimuth was computed by taking the mean arctangent of the x and y particle velocity vectors in short (1 ms) windows. Similarly, elevation was computed by taking the arctangent of the z vector over the square root of the sum of the x and y vectors squared in the same short windows.

To put these data in context, field-based particle motion values are not often published, thus comparisons are difficult. However, the authors recently made measurements of coral reefs and the surrounding area in Maui, HI (very near this field site) [15]. Our reef sound pressure values were overall lower than those of very loud choruses measures elsewhere [5-7]; (also the propagation conditions were likely very different). However, particle motion values were ca. -90 dB re 1 m/s2) acceleration at 500 Hz. Velocity values were ca. -125 dB re 1 m/s (full band).



Supplementary Figure 1. Bandpass filtered elevation and azimuth values for a 21 s portion of humpback whale song (shown in the spectrogram in Figure 1; and as an unfiltered signal in Figure 2). The bandwidth of the filter is listed at the top of each subfigure (A, B, C, D). The data show that the highest amplitude portions of the cue were found in the lowest frequencies surrounding the fundamental portion of the song (100-300 Hz), whereas higher frequency harmonics (300-500 and 500-1000 Hz) showed little contribution to overall amplitude of the signal. Note, the z-axes ranges differ for elevation and azimuth.



Supplementary Figure 2. Schematic of deployed M20 sensor with azimuth and elevation noted.

Supplemental References

[1]Nedelec, S.L., Radford, A.N., Simpson, S.D., Nedelec, B., Lecchini, D. & Mills, S.C. 2014 Anthropogenic noise playback impairs embryonic development and increases mortality in a marine invertebrate. *Scientific reports* **4**.
[2]Kaplan, M.B. & Mooney, T.A. 2016 Coral reef soundscapes do not propagate that far. *Scientific Reports* **6**, 31862. (doi:10.1038/srep31862).
[3]Nedelec, S.L., Campbell, J., Radford, A.N., Simpson, S.D. & Merchant, N.D. 2016 Particle motion: the missing link in underwater acoustic ecology. *Methods Ecol. Evol.*
[4]Martin, B., Zeddies, D.G., Gaudet, B. & Richard, J. 2016 Evaluation of three sensor types for particle motion measurement. In *The Effects of Noise on Aquatic Life II* (pp. 679-686, Springer.
[5]Cato, D.H. 1980 Some unusual sounds of apparent biological origin responsible for sustained background noise in the Timor Sea. *The Journal of the Acoustical Society of America* **68**, 1056-1060.
[6]Radford, C.A., Stanley, J.A., Tindle, C.T., Montgomery, J.C. & Jeffs, A.G. 2010 Localised coastal habitats have distinct underwater sound signatures. *Mar. Ecol. Prog. Ser.* **401**, 21-29. (doi:doi: 10.3354/meps08451).
[7]Radford, C.A., Tindle, C.T., Montgomery, J.C. & Jeffs, A.G. 2011 Modelling a reef as an extended sound source increases the predicted range at which reef noise may be heard by fish larvae. *Mar. Ecol. Prog. Ser.* **438**, 167-174. (doi:doi: 10.3354/meps09312).